Adjustment to climate change is constrained by arrival date in a long-distance migrant bird

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Table 1 Subduction zone carbon budget

Subducted carbon (Tmol yr^{-1})*	
Sediment carbonate[6]	1.2
Sediment organic carbon[1]	0.8
Oceanic metabasalts[19]	3.4
Total	5.4
Expelled carbon (Tmol yr^{-1})	
Arc magmatism[20]	2–3
Carbon imbalance† (Tmol yr^{-1})	2.5–3.5

*1 Tmol = 10^{12} mol.
† (Subducted carbon) – (expelled carbon).

basalts is expected in subarcs. Barring extensive infiltration of externally derived fluids, our study implies marked devolatilization under forearcs (for clay-rich marls with high-temperature geotherms) or retention of H_2O and CO_2 to depths well beyond subarcs (for siliceous limestones in all geotherms and clay-rich marls with low-temperature geotherms). Accordingly, most of the initial CO_2 and H_2O in subducted marine sediments will not be released beneath volcanic arcs. This inference is consistent with both the deficiency in the amount of CO_2 released from arc volcanoes compared to the amount of CO_2 contained within subducted carbonates (Table 1) and with the imbalance between subducted versus expelled H_2O (ref. 1).

Our equilibrium analysis implicitly assumes that there is no significant kinetic overstepping and metastability of metamorphic reactions. Although significant disequilibrium has been suggested for the transformation of anhydrous oceanic basalts and gabbros to eclogites[15], the catalytic effect of H_2O (ref. 15) implies that equilibrium is more likely in dehydrating systems such as subducted sediments.

Melting is an alternative mechanism for release of volatiles from subducted sediment. Recent experiments using marine red clay[16] suggest that sediment melting does not occur for the geotherms that we consider here. However, because metastable starting materials (for example, red clay) are unsuitable models for subduction-zone metamorphism and melting, confirmation of this conclusion requires experiments with more realistic initial mineral assemblages. Dissolution of minerals in supercritical fluids remains a possible, albeit largely unquantified, alternative mechanism for devolatilization.

As shown in Fig. 2, fluids produced by metamorphism of subducted marine sediments are H_2O-rich. Consequently, expulsion of such fluids to the overlying mantle wedge would not substantially affect the P–T conditions of melting (solidus) of the mantle wedge compared to those expected in the presence of a pure H_2O fluid.

Devolatilization of subducted sediment could contribute to seismicity along the tops of subducted slabs. The continuous nature of devolatilization is compatible with the spread of earthquake hypocentres along individual subduction zones[17]. However, correlation of slab seismicity with metamorphic devolatilization of subducted sediments needs to consider the marked differences in devolatilization for different bulk compositions and geotherms. □

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1. Bebout, G. E. The impact of subduction-zone metamorphism on mantle-ocean chemical cycling. *Chem. Geol.* **126,** 191–218 (1995).
2. Kerrick, D. M. & Connolly, J. A. D. Subduction of ophicarbonates and recycling of CO_2 and H_2O. *Geology* **26,** 375–378 (1998).
3. Yaxley, G. M. & Green, D. H. Experimental demonstration of refractory carbonate-bearing eclogite and siliceous melt in the subduction regime. *Earth Planet. Sci. Lett.* **128,** 313–325 (1994).
4. Molina, J. F. & Poli, S. Carbonate stability and fluid composition in subducted oceanic crust: an experimental study on H_2O-CO_2 bearing basalts. *Earth Planet. Sci. Lett.* **176,** 295–310 (2000).
5. Domanik, K. J. & Holloway, J. R. Experimental synthesis and phase relations of phengitic muscovite from 6.5 to 11 GPa in a calcareous metapelite from the Dabie Mountains, China. *Lithos* **52,** 51–77 (2000).
6. Caldeira, K. Continental-pelagic carbonate partitioning and the global carbonate-silicate cycle. *Geology* **19,** 204–206 (1991).
7. Kerrick, D. M. & Connolly, J. A. D. Metamorphic devolatilization of subducted oceanic metabasalts: Implications for seismicity, arc magmatism and volatile recycling. *Earth Planet. Sci. Lett.* (in the press).
8. Plank, T. & Langmuir, C. H. The chemical composition of subducting sediment and its consequences for the crust and mantle. *Chem. Geol.* **145,** 325–394 (1998).
9. Connolly, J. A. D. Multivariable phase diagrams: an algorithm based on generalized thermodynamics. *Am. J. Sci.* **290,** 666–718 (1990).
10. Holland, T. & Powell, R. An internally consistent thermodynamic data set for phases of petrologic interest. *J. Metamorph. Geol.* **16,** 309–343 (1998).
11. Holland, T. & Powell, R. A compensated Redlich-Kwong (CORK) equation for volumes and fugacities of CO_2 and H_2O in the range 1 bar to 50 kbar and 100-1600°C. *Contrib. Mineral. Petrol.* **109,** 265–273 (1991).
12. Peacock, S. M. & Wang, K. Seismic consequences of warm versus cool subduction metamorphism: Examples from Southwest and Northeast Japan. *Science* **286,** 937–939 (1999).
13. Becker, H. & Altherr, R. Evidence from ultra-high-pressure marbles for recycling of sediments into the mantle. *Nature* **358,** 745–748 (1992).
14. Schmidt, M. W. & Poli, S. Experimentally based water budgets for dehydrating slabs and consequences for arc magma generation. *Earth Planet. Sci. Lett.* **163,** 361–379 (1998).
15. Hacker, B. R. in *Subduction Top to Bottom* (eds Bebout, G. E., Scholl, D. W., Kirby, S. H. & Platt, J. P.) 337–346 (Monograph 96, American Geophysical Union, Washington DC, 1996).
16. Johnson, M. C. & Plank, T. Dehydration and melting experiments constrain the fate of subducted sediments. *Geochem. Geophys. Geosyst.* **1,** 1525–2027 (1999).
17. Kirby, S., Engdahl, E. R. & Denlinger, R. in *Subduction Top to Bottom* (eds Bebout, G. E., Scholl, D. W., Kirby, S. H. & Platt, J. P.) 195–214 (Monograph 96, American Geophysical Union, Washington DC, 1996).
18. Tatsumi, Y. & Eggins, S. *Subduction Zone Magmatism* (Blackwell Scientific, Oxford, 1995).
19. Alt, J. C. & Teagle, D. A. H. The uptake of CO_2 during alteration of the ocean crust. *Geochim. Cosmochim. Acta* **63,** 1527–1535 (1999).
20. Marty, B. & Tostikhin, I. N. CO_2 fluxes from mid-ocean ridges, arcs and plumes. *Chem. Geol.* **145,** 233–248 (1998).

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Adjustment to climate change is constrained by arrival date in a long-distance migrant bird

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Spring temperatures in temperate regions have increased over the past 20 years[1], and many organisms have responded to this increase by advancing the date of their growth and reproduction[2–7]. Here we show that adaptation to climate change in a long-distance migrant is constrained by the timing of its migratory journey. For long-distance migrants climate change may advance the phenology of their breeding areas, but the timing of some species' spring migration relies on endogenous rhythms that are not affected by climate change[8]. Thus, the spring migration of these species will not advance even though they need to arrive earlier on their breeding grounds to breed at the appropriate time. We show that the migratory pied flycatcher *Ficedula hypoleuca* has advanced its laying date over the past 20 years. This temporal shift has been insufficient, however, as indicated by increased selection for earlier breeding over the same period. The shift is hampered by its spring arrival date, which has not advanced. Some of the numerous long-distance migrants will suffer from

climate change, because either their migration strategy is unaffected by climate change, or the climate in breeding and wintering areas are changing at different speeds, preventing adequate adaptation.

Higher spring temperatures over the past two decades have led to advancing tree phenology and subsequently to earlier peaks in insect abundance[9–11]. Several bird species[3,4], but not all[9,12], have advanced their egg-laying date as a consequence of this advancement in their food supply[4–7,9]. Advancement of laying has not kept up with selection for earlier laying in areas where early spring temperatures have not increased as much as those late in spring[9,13]. Adaptive advancement of reproduction may also be hampered in species that rely on endogenous rhythms or environmental stimuli unrelated to temperature[8], such as day length. Long-distance migrants are extremely vulnerable in this sense, because in some well-studied species the timing of spring migration from the overwintering area is triggered by cues that are unlinked to the climate at their breeding grounds, and their breeding date is constrained by their arrival date.

We examined how a long-distance migrant bird, the pied flycatcher *Ficedula hypoleuca*, has responded to recent climate change, using data from a long-term study in the Hoge Veluwe (The Netherlands). Pied flycatchers overwinter in the zone of dry tropical forest at about 10° north in west Africa, and breed in temperate forests in Europe[14]. Males normally arrive before females, and females select males on the quality of their territory[15].

Temperatures at the time of arrival and the start of breeding by pied flycatchers (16 April to 15 May) have increased significantly over the period 1980–2000 (Fig. 1a). Over the same period, the birds have not advanced the spring arrival on their breeding grounds (Fig. 1b), but have advanced their mean laying date by about 10 days (Fig. 1c). Mean laying date was unrelated to population size[16], and population size did not show a significant trend ($r = -0.08$, $n = 21$, $P = 0.72$). Selection for early laying date has become stronger over the course of this 20-year period (Fig. 1d), indicating that early laying pairs do better than later pairs. Thus, the response in laying date has not been sufficiently strong to track the advancement of spring.

Mean laying date was strongly correlated with the mean temperature in the second half of April and the first half of May (Fig. 2a), but arrival date was not (Fig. 2b). Arrival and laying dates were furthermore uncorrelated with temperatures in the first half of April, just before arrival of most birds (arrival: $r = -0.04$, $n = 20$, $P = 0.87$; laying: $r = 0.30$, $n = 21$, $P = 0.20$). The advancement of egg-laying date was, to a large extent, caused by plasticity of individual females to temperature[12] (analysis of covariance (ANCOVA): individual, $F_{272,411} = 2.16$, $P < 0.001$; age, $F_{1,412} = 17.12$, $P < 0.001$; temperature, $F_{1,412} = 50.57$, $P < 0.001$; average individual slope (-1.10 ± 0.15) significantly differs from population slope (-1.67 ± 0.24), $F_{1,413} = 13.55$, $P < 0.001$), and not by selection for genotypes for early breeding (heritability[17] (h^2) for laying date (relative to yearly mean) calculated from mother–daughter regression is not significant: $F_{1,225} = 1.11$, $P = 0.29$, $h^2 = 0.16 \pm 0.15$). As a consequence of the correlation between laying and temperature (Fig. 2a) and the absence of a correlation between arrival date and temperature (Fig. 2b), the interval between arrival and egg-laying has decreased with increasing temperatures (linear regression: $F_{1,19} = 9.73$, $P = 0.006$).

Pied flycatchers were able to advance their laying date because they normally arrive on their breeding grounds earlier than their average optimal laying date[14]. Their spring migration strategy, triggered by day-length variation on their wintering grounds[8], enabled them to arrive in time to respond adaptively to the naturally occurring variation in the start of spring[18], and thereby start egg-laying at the date that maximizes fitness[9]. Owing to the advanced phenology on their breeding grounds and their relatively inflexible arrival date, however, this window has become too narrow, and a significant part of the population is now laying too late to exploit the peak in insect abundance optimally (as shown by the increasing selection for early laying; Fig. 1d).

The strong response of laying date in the pied flycatcher seems at variance with the lack of response in the resident great tit *Parus major* population breeding in the same area[9]. In both cases, however, the advancement of laying date is insufficient, as indicated by the presence of increased selection for earlier breeding. For the great tits, which start egg-laying about 2 weeks earlier than the flycatchers, the lack of a sufficient response is due to increasing temperatures in late, but not in early spring. For the flycatchers, the advancement is not hampered by such temporal variation in climate change, but because their timing of spring migration is triggered by day length, which is not affected by spring temperatures on their breeding grounds. The decision when to start spring migration thus becomes maladaptive if the cue used for migration is independent of the environmental change in the breeding area.

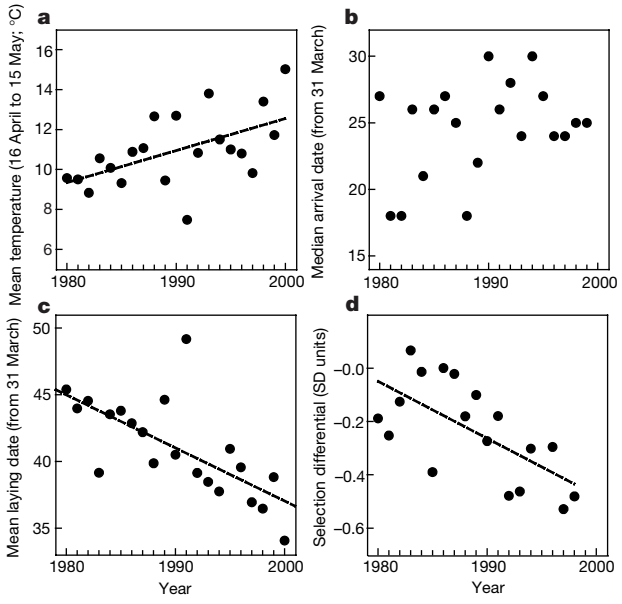

Figure 1 Spring temperature, breeding and spring arrival date of a pied flycatcher population in the Netherlands from 1980 to 2000. **a**, Mean average daily temperature in the period of arrival increased (linear regression: $F_{1,19} = 8.31$, $P < 0.001$). **b**, Median arrival date did not advance ($F_{1,19} = 2.32$, $P = 0.15$). **c**, Mean laying date did advance ($F_{1,20} = 17.14$, $P < 0.001$). **d**, Standardized selection differential for laying date decreased with year ($F_{1,17} = 12.00$, $P = 0.003$) over this period.

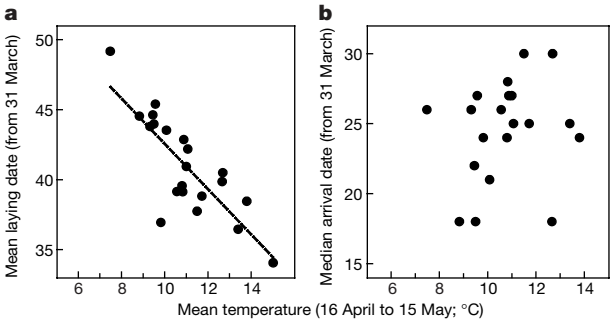

Figure 2 Breeding date and spring arrival of a pied flycatcher population as a function of spring temperature in the Netherlands. **a**, Average laying date was significantly related to the mean average daily temperature (°C) in the second half of April and the first half of May ($F_{1,20} = 37.59$, $P < 0.001$). **b**, Median arrival date was unrelated to spring temperature ($F_{1,19} = 0.66$, $P = 0.43$).

In other long-distance migrants, arrival on the breeding grounds is also relatively insensitive to the temperature on arrival[19], although in some species the temperature on journey is a good correlate of arrival date[20,21]. Climatic factors may be important in fine-tuning the onset and speed of migration, but climate change differs between temperate and tropical latitudes[1], and therefore a response to environmental cues such as temperature for the onset and speed of migration may not lead to an adequate arrival date on the breeding grounds. Short-distance migrants may be more flexible in their response, because the circumstances on the wintering grounds will be a better predictor for the optimal arrival time on the breeding grounds and genetic variation has been shown for some of their migratory traits[22,23].

Large-scale climate change may thus form a serious threat to at least some of the numerous species that migrate from tropical wintering grounds to temperate breeding areas[24], because they arrive at an inappropriate time to exploit the habitat optimally, and face higher competition with resident species that may have increased in numbers through enhanced winter survival[25]. This may, in fact, be partly responsible for the decline of these species in western Europe[26]. □

Methods

Data collection

Data were collected from a nest-box breeding population of pied flycatchers in the Hoge Veluwe area, central Netherlands, between 1965 and 2000 (ref. 9). We analysed data from 1980 to 2000, because temperature increased most markedly after 1980. We used only nests that were considered to be first nesting attempts of females during that year ($n = 1,892$). Parents and chicks were ringed with uniquely numbered aluminium rings. Arrival data were obtained from a local amateur bird group, working within 10 km from the study area[27]. Members of this bird group recorded each year the first singing pied flycatcher, and the median first arrival date was used as approximation of arrival in the study area. The lack of an advancement in arrival date was confirmed by analysing the arrival date of the first male recorded in the study area from 1992 to 2000 ($F_{1,6} = 0.26$, $P = 0.63$), the first ten males that arrived in an area nearby from 1980 to 1990 ($F_{1,10} = 0.02$, $P = 0.88$), and the mean start of nest building of the first ten pied flycatcher nests each year in 1980–2000 ($F_{1,19} = 0.92$, $P = 0.35$; start of egg-laying was estimated from the state of the nest during weekly checks).

Analyses

All analyses were performed with linear regression using two-tailed P values. In most cases we used annual means. In the analysis of the response of individual females to temperature, we used females that bred in at least 2 years ($n = 273$). In this analysis, female age was a factor for first known breeding or later breeding in the area (real age was not determined), because first year breeders normally breed later[14]. Individual is used here as a factor in an ANCOVA. Temperature used is the average of the mean daily temperatures from 16 April to 15 May recorded by the Royal Dutch Meteorological Institute (KNMI) at De Bilt (The Netherlands). The standardized selection differential is the mean laying date weighted for the number of recruits (offspring that return as breeding birds in the study area) each nest produced minus the mean laying date, divided by the standard deviation of laying date[17]. Selection differentials are given until 1998, because the number of recruits for later years is not yet known.

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1. Houghton, J. T. *et al.* (eds) *Climate Change 1995* (Cambridge Univ. Press, Cambridge, 1996).
2. Beebee, T. J. C. Amphibian breeding and climate. *Nature* **374,** 219–220 (1995).
3. Crick, H. Q. P., Dudley, C., Glue, D. E. & Thomson, D. L. UK birds are laying eggs earlier. *Nature* **388,** 526 (1997).
4. Crick, H. Q. P. & Sparks, T. H. Climate change related to egg-laying trends. *Nature* **399,** 423–424 (1999).
5. Forchhammer, M. C., Post, E. & Stenseth, N. C. Breeding phenology and climate. *Nature* **391,** 29–30 (1998).
6. McCleery, R. H. & Perrins, C. M. …temperature and egg-laying trends. *Nature* **391,** 30–31 (1998).
7. Brown, J. L., Li, S. H. & Bhagabati, N. Long-term trend toward earlier breeding in an American bird: a response to global warming? *Proc. Natl Acad. Sci. USA* **96,** 5565–5569 (1999).
8. Gwinner, E. Circannual clocks in avian reproduction and migration. *Ibis* **138,** 47–63 (1996).
9. Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. Lond. B* **265,** 1867–1870 (1998).
10. Harrington, R., Woiwod, I. & Sparks, T. H. Climate change and trophic interactions. *Trends Ecol. Evol.* **14,** 146–150 (1999).
11. Visser, M. E. & Holleman, L. J. M. Warmer spring disrupt the synchrony of Oak and Winter Moth phenology. *Proc. R. Soc. Lond. B* **268,** 289–294 (2001)
12. Przybylo, R., Sheldon, B. C. & Merila, J. Climatic effect on breeding and morphology: evidence for phenotypic plasticity. *J. Anim. Ecol.* **69,** 395–403 (2000).
13. Stevenson, I. R. & Bryant, D. M. Climate change and constraints on breeding. *Nature* **406,** 366–367 (2000).
14. Lundberg, A. & Alatalo, R. V. *The Pied Flycatcher* (T. & A. D. Poyser, London, 1992).
15. Alatalo, R. V., Lundberg, A. & Glynn, C. Female Pied Flycatchers choose territory quality and not male characteristics. *Nature* **323,** 152–153 (1986).
16. Both, C. Density dependence of avian clutch size in resident and migrant species: is there a constraint on the predictability of competitor density? *J. Avian Biol.* **31,** 412–417 (2000).
17. Falconer, D. S. & Mackay, F. T. C. *An Introduction to Quantative Genetics* 4th edn (Longman Higher Education, Essex, 1996).
18. Buse, A., Dury, S. J., Woodburn, R. J. W., Perrins, C. M. & Good, J. E. G. Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Funct. Ecol.* **13** (suppl. 1), 74–82 (1999).
19. Mason, C. F. Long term trends in the arrival dates of spring migrants. *Bird Study* **42,** 182–189 (1995).
20. Huin, N. & Sparks, T. H. Spring arrival patterns of the Cuckoo *Cuculus canorus*, Nightingale *Luscinia megarhynchos* and Spotted Flycatcher *Musciapa striata* in Britain. *Bird Study* **47,** 22–31 (2000).
21. Huin, N. & Sparks, T. H. Arrival and progression of the Swallow *Hirundo rustica* through Britain. *Bird Study* **45,** 361–370 (1998).
22. Berthold, P., Helbig, A. J., Mohr, G. & Querner, U. Rapid microevolution of migratory behaviour in a wild bird species. *Nature* **360,** 668–670 (1992).
23. Pulido, F., Berthold, P. & van Noordwijk, A. J. Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. *Proc. Natl Acad. Sci. USA* **93,** 14642–14647 (1996).
24. Berthold, P., Fiedler, W., Schlenker, R. & Querner, U. 25-year study of the population development of Central European songbirds: A general decline, most evident in long-distance migrants. *Naturwissenschaften* **85,** 350–353 (1998).
25. Berthold, P. Patterns of avian migration in light of current global 'greenhouse' effects: a central European perspective. *Acta XX Congressus Internationalis Ornithologici* 780–786 (1990).
26. Myers, J. P. & Lester, R. T. *Global Warming and Biodiversity* (eds Peters, R. L. & Lovejoy, T. E.) 193–200 (Yale Univ. Press, New Haven, 1992).
27. Pilzecker, J. Een voorjaar maakt nog geen fenologie; Bewerking van de fenologiegegevens van Vogelwerkgroep Arnhem e. o. over de periode 1980–1997. Report No. 98-2 (Vogelwerkgroep Arnhem e. o., Arnhem, 1998).

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Endosymbiotic sulphate-reducing and sulphide-oxidizing bacteria in an oligochaete worm

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Stable associations of more than one species of symbiont within a single host cell or tissue are assumed to be rare in metazoans because competition for space and resources between symbionts can be detrimental to the host[1]. In animals with multiple endosymbionts, such as mussels from deep-sea hydrothermal vents[2] and reef-building corals[3], the costs of competition between the symbionts are outweighed by the ecological and physiological flexibility gained by the hosts. A further option for the coexistence of multiple symbionts within a host is if these benefit directly from one another, but such symbioses have not been previously described. Here we show that in the gutless marine oligochaete